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THE EMBRYOGENY OF CYRTANTHUS PARVIFLORUS BAKER

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(Received for publication April 7, 1921)

Introduction

The question of the relationship of monocotyledonous and dicotyledonous plants, long and hotly debated and yet unsettled, has of late years largely been attacked from two angles, the sequence and position of organ formation in the early developing embryo, and the vascularization of the seedling. The origin of the monocotyledonous type from the primitive dicotyledons at one or more points seems an established probability, but the stages of the transfer from the one into the other have not been completely filled out, and apparent anomalies will remain until we have knowledge of a vastly greater series of forms than at present.

In 1917 the writer began the preservation and sectioning of material of *Cyrtanthus parviflorus* Baker, with the principal object of securing a complete series of embryo-sac and embryo stages for demonstration purposes. The work had proceeded for some time before he came upon the paper of Miss Farrell on the related *Cyrtanthus sanguineus* (Lindl.) Hook., when it was at once evident that the embryological history in the two forms is vastly different. From time to time more material of *Cyrtanthus parviflorus* was prepared, until at present a practically unbroken series of stages has been secured from fertilization to seed maturity. Young seedlings have also been sectioned to follow the history of the vascular bundles and other structures in germination. Although this species does not present any new situation in monocotyledonous embryogeny, the completeness of the material and the variation it would seem to indicate within a single genus will perhaps warrant the presentation of this description as a little evidence toward a solution of the major problem.

Material and Observations

Under greenhouse culture the plants practically never set seed unless hand-pollinated; this rendered unnecessary the castration and bagging of the flowers. Fixations followed at suitable intervals after pollination, and full records of dates and of time elapsed were preserved. About fifty post-fertilization fixations were made and studied, in addition to a lesser number dealing with the maturation of the pollen and of the embryo sac.

Fertilization follows pollination in from 36 to 50 hours, seeming to vary somewhat in the different batches. The egg is enclosed in a definite membrane at the micropylar end of the sac and is fertilized in that position;

the polar nuclei have united during the maturation of the embryo sac and have passed to the antipodal end where the triple fusion occurs. Both zygote and primary endosperm nuclei then remain in a state of rest with finely divided extra-nucleolar chromatin for some time. Three or four successive divisions of the endosperm nucleus precede the first division of the zygote, which occurs in from 94 to 118 hours after pollination. The first and second endosperm mitoses occur close to the antipodals at the base of the embryo sac, but the nuclei produced soon move down along the sides of the sac and with subsequent free nuclear divisions become equally distributed in the peripheral cytoplasm. The sac is large and increases in size rapidly after fertilization, so that there seems to be no evidence of pressure upon the embryo until centripetal wall formation occurs in the endosperm, after all parts of the embryo have become well established (4, p. 433).

The first divisions of the zygote give rise to a filament of three, occasionally four, cells (figs. 1, 2, 3). Then transverse divisions and vertical walls occur in the terminal and subterminal cells of the row (fig. 4). The lowest cell is primarily concerned in the formation of the suspensor, which is unicellular or divided at the top by one to three more or less oblique walls (figs. 5, 9). The embryo proper develops as an ovoid mass until it has attained a length of 8–10 cells, when it becomes evident that the structure is no longer radially symmetrical, but that it has developed a bilateral symmetry, one side being more convex than the other (figs. 5, 6, 7, 8). All the tissue beyond the point of indentation becomes the cotyledon, which seems to be derived from the end cell of the primitive row. It seems equally clear that the root is derived from the middle cell, but the conditions in the region of the growing point are not so certain. The swelling on the lower portion of the indentation gives rise first to an outer ridge that connects with the cotyledon on the sides, and subsequently, within and protected by this ridge, to a series of 2 or 3 plumular leaves (figs. 9, 10, 11).

The first sign of the development of the vascular system appears at the same time as the first plumular leaf, in the form of a pair of bundles in the cotyledon (fig. 13). These soon join with the rudiment of the axial system at the cotyledonary node. In the old embryo this node has four principal poles, two connected with the bundles which traverse the cotyledon, two with bundles which run forward and curve up, joining with the main cotyledonary traces above the tip of the plumule. These loops first appear near their attachment at the node, and subsequently effect union with the main trace (figs. 16, 17, 19). The rudiment of a single bundle appears in the older plumular leaf before germination (figs. 18, 20). As the size of the embryo increases, the ridge early formed connecting the edges of the cotyledon elongates and widens, forming with the cotyledon a short sheath around the plumule. The base of the cotyledon becomes quite broad and curved so that the looped bundle traces appear in a transverse section to lie opposite, or even a little in front of, the edges of the first leaf (fig. 23). With germination the basal sheathing portion of the cotyledon containing the vascular loops elongates greatly, so that the foliage leaves issue from a long tubular cotyledonary sheath (figs. 22, 24, 25).

Discussion

The first question which arises in the consideration of plants, for which there is reported so different a history of a conservative structure, is the degree of relationship of the forms. *Cyrtanthus sanguineus* (Lindl.) Hook. was the first described (6). It belongs to the subgenus Gastronema, which by some has been considered as of generic rank. However, the points that distinguish this subgenus are but slight and quantitative rather than qualitative, the flowers being fewer, larger, and more erect than in the other subgenera. *Cyrtanthus parviflorus* was described by Baker in 1891 (1). In the *Flora Capensis* of Thiselton-Dyer he places it in the subgenus Monella which differs from the subgenus Cyrtanthus chiefly in having linear rather than lorate leaves (9). There is little from the systematic standpoint, therefore, to indicate that the forms are not closely related.

The first paper touching upon the embryo of *Cyrtanthus sanguineus* was that of Miss Farrell in May, 1914 (4). In June of the same year Coulter and Land gave some additional details (2). The condition in *Cyrtanthus sanguineus* as interpreted by these writers is, briefly, as follows: At the top of the ovoid proembryo arise four swellings or growing points. These are soon followed by a ring of growth upon which they are raised up as upon a tube. Then they merge in twos by an active growth of the tissue between the pairs. Subsequently one duplex structure greatly outgrows the other, forming the prominent cotyledon, while the other, which does not shoot up, with the tubular portion constitutes the sheath. For her paper, Miss Farrell had available but two stages of embryo material, one showing the tubular stage with the swellings on the rim, the other a nearly mature embryo. This would seem a very small amount on which to base the important conclusions at which she arrives. Coulter and Land appear to have had additional material, though they do not figure it. As a result of their observations on embryos, Coulter and Land conclude in part as follows:

> In the embryogeny of both monocotyledons and dicotyledons, a peripheral cotyledonary zone gives rise to two or more growing points, or primordia; this is followed by zonal development, resulting in a cotyledonary ring or sheath of varying length. If both growing points continue to develop equally, the dicotyledonous condition is attained; if one of the growing points ceases to develop, the continued growth of the whole cotyledonary zone is associated with that of the other growing point, and the monocotyledonous condition is attained. In like manner, polycotyledony is simply the appearance and continued development of more than two growing points on the cotyledonary ring. It follows that cotyledons are always lateral structures, arising from the peripheral zone developed at the top of the more or less massive proembryo (3).

In *Cyrtanthus parviflorus* it seems fairly clear to the writer that the cotyledon originates now as a terminal structure, no matter what, evolutionarily, its status may have been. The growing point forms well down on one side of the embryo, its location presaged by the smaller size of the cells and their denser protoplasmic contents before indentation becomes evident. As a semilunar ridge on the lower side of the meristematic region there arises a sheath which, joined with the base of the cotyledon, functions as do the sheathing bases of many other monocotyledonous leaves. The mature stage of *Cyrtanthus sanguineus* agrees closely with that of *Cyrtanthus parviflorus*. The writer would consider that the species he has studied corresponds through its early stages in all essentials with the familiar cases of Alisma (5) and Sagittaria (8), and that it does not lend support to the view of Coulter and Land quoted above.

With regard to the general question of the origin of the monocotyledonous type, this form, as an isolated case, can add little. Its vascular anatomy is easily connected with that of other Amaryllidaceous types previously described (7), but gives no decisive evidence for or against the theory of the origin of the single cotyledon by the edge-to-edge union of the two dicotyledonous seed leaves. Worsdell seems to consider that the condition in *Cyrtanthus sanguineus* is an abnormal one, an example of a minor instance of progressive evolution (10). Whether it is an isolated case, or connected with the more ordinary *Cyrtanthus parviflorus* by intermediate stages, it remains for a wider study of the genus to demonstrate.

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DESCRIPTION OF FIGURES

PLATE XXV

FIGS. 1–4. Fertilized egg and filamentous stage of the proembryo. × 150. Figure 1, 65 hours after pollination; figures 2, 3, 332 hours, figure 4, 284 hours after pollination.

FIGS. 5–8. Development of the bilaterally symmetrical embryo. × 150. Sagittal sections. Figure 5, 294 hours after pollination; figure 6, 428 hours, figure 7, 480 hours, figure 8, 600 hours after pollination.

FIGS. 9–10. Formation of the lateral growing point, sagittal sections. × 150. Figure 9, 480 hours, figure 10, 600 hours after pollination.

FIGS. 11–12. Origin of the sheath and of the first leaf, sagittal sections. × 75. Figure 11, 576 hours, figure 12, 648 hours after pollination.

PLATE XXVI

FIGS. 13–20. Stages in the development of the vascular strands and of sheath and leaf. Figures 13, 19, frontal sections; figures 14, 15, 17, 18, 20, sagittal; figure 16, intermediate. × 30. Figures 13, 14, 648 hours, figure 15, 576 hours after pollination; figure 16, age unknown; figure 17, 762 hours, figures 18, 19, 20, 888 hours after pollination. All are reconstructions from several serial sections. Figure 16 shows a case where one of the loops has failed to develop. The partial suppression of one loop was observed on several occasions.

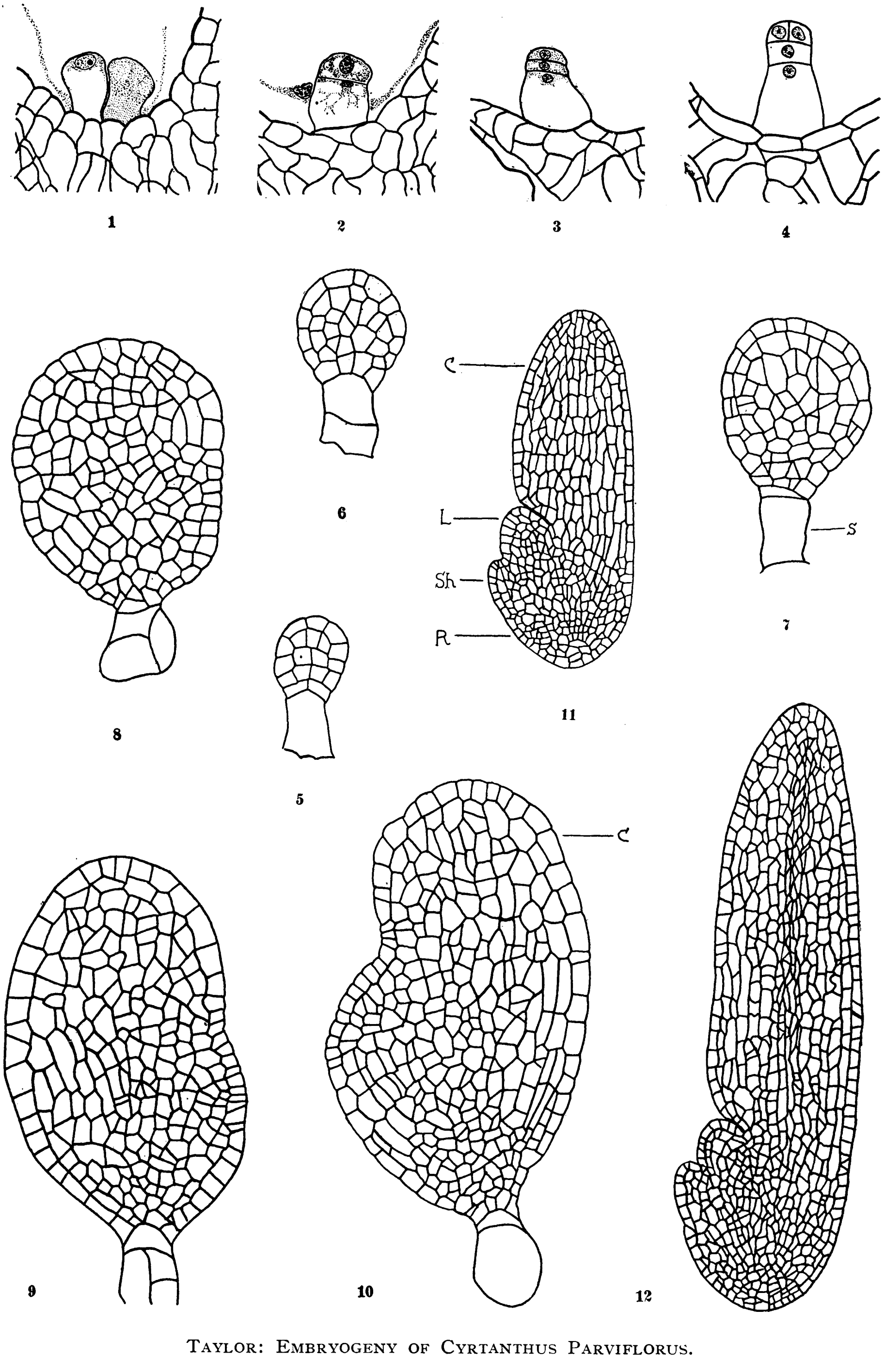
FIG. 21. Surface view of embryo showing the sheath and the first leaf. The shapes of the cells at the margin of the sheath and in the leaf and surrounding portion of the cotyledon have been indicated. × 90.

FIG. 22. Front view of sheath. The cotyledon was split sagittally from the rear and the sheathing base was spread out on the slide. All cut edges indicated by broken lines; vascular bundles by dotted lines. × 9.

FIG. 23. Transverse section of cotyledon and sheath. This shows the positions of the vascular bundles and of the first leaf. × 75.

FIGS. 24, 25. Seedlings, about two weeks after germination. These show the length of the sheath. In figure 24 the seed has been entirely removed from the absorbing cotyledon, but in figure 25, although the seed coats have been removed, the endosperm is intact. Vascular bundles indicated by dotted lines. × 3.

"*S*" suspensor, "*R*" radicle, "*Sh*" sheath, "*L*" first leaf, "*C*" cotyledon, "*E*" endosperm.



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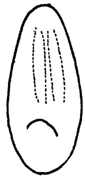

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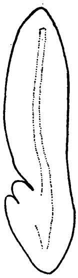

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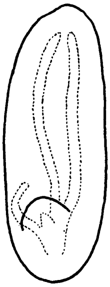

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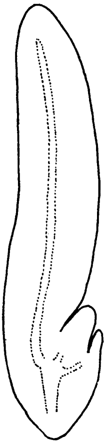

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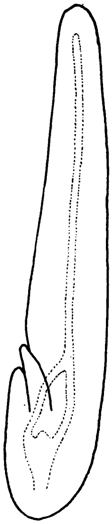

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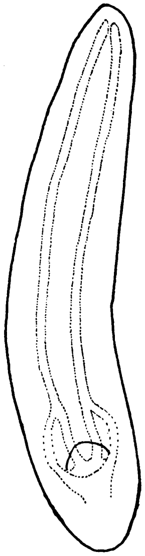

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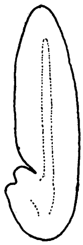

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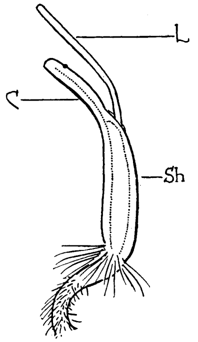

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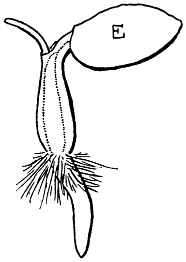

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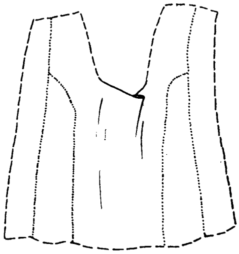

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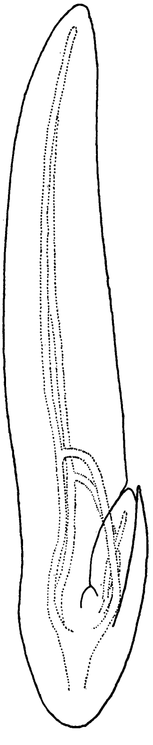

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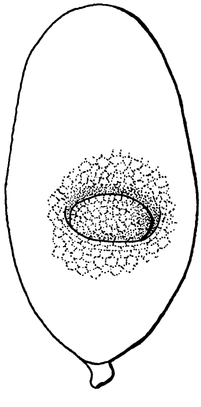

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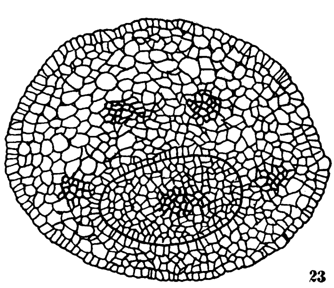

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